THE PROTHONOTARY WARBLER

POPULATION VIABILITY AND CRITICAL HABITAT IN SOUTHERN ONTARIO, CANADA

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Summary

The Prothonotary Warbler was designated as “Endangered” Species in 2000 by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). The species at risk act (SARA) prescribes identification and protection of critical habitat for this species. This work contributes to and supplements related recovery and conservation efforts. A comprehensive population and habitat viability analysis has been conducted for the Prothonotary Warbler in the Carolinian region in southern Ontario. Metapopulation and individual-based, spatially explicit population models were used to asses demographic viability, minimum viable population size, dependency on immigration from external populations, susceptibility to habitat loss and fragmentation and critical habitat for the Prothonotary Warbler population. The results indicate that the Prothonotary Warbler population in southern Ontario may be demographically limited due to either climatic constraints or factors associated with habitat quality. The observed fecundity may not completely compensate the observed survival probability resulting in a declining population. The minimum viable population size for a time frame of 20 years is estimated to be 80 breeding pairs. The current population size of 24 breeding pairs is far less and would ensure a viable population for a time frame of less than 10 years. These model predictions contradict the observed stability in the population size over the last few years. One assumption has been that the lack of self-sustainability in the Prothonotary Warbler population in southern Ontario may be offset by immigrants from external populations. Results of simulation experiments show that one immigrating breeding pair every 2 years may be sufficient to eliminate the extinction risk. The viability of the Prothonotary Warbler population may generally increase with increasing habitat amount and may decrease with habitat fragmentation. The effect of habitat fragmentation on extinction risk increases with decreasing habitat amount. Despite these general effects, it is unlikely that the particular habitat configuration in southern Ontario constitutes a limiting factor for the Prothonotary Warbler population. In fact, the results of the population models indicate that the Prothonotary Warbler may be unable to utilize all suitable habitat, even though its observed dispersal capability of up to 120 km. Critical habitat has been identified based on simulating the population dynamic of the Prothonotary Warbler on a habitat suitability map. The habitat suitability map is the result of a logical combination of different data layers known to affect the occurrence of the Prothonotary Warbler. Habitat patch removal experiments revealed those critical habitat areas, which are most important to the viability of the Prothonotary Warbler population. The Rondeau Provincial Park and Amherstburg in Essex county are most critical for the Prothonotary Warbler based on its observed distribution in 2002. Other habitat areas have lower but also substantial effects on the population viability and may become more important when the population distribution changes. To summarize, the Prothonotary Warbler population in southern Ontario is not self-sustainable and may become extinct without a continuous influx from external populations. Habitat amount is not likely to be a limiting factor but critical habitat areas must be protected here and elsewhere to ensure a long-term survival of the Prothonotary Warbler in Canada.

List of contents

Summary 1
List of contents 2
1 Prothonotary Warbler *(Protonotaria citrea)* 3
1.1 Demography 3
1.2 Population Model 3
1.2.1 Model Characteristics 3
1.2.2 Parameter Values 4
1.2.3 Analysis of the demographic population viability (non-spatial) 4
1.2.4 Immigration and demographic viability 6
1.2.5 Habitat Configuration Analysis 7
1.3 Critical Habitat Analysis 10
1.3.1 Habitat Suitability Map 10
1.3.2 Source – Sink habitat 11
1.3.3 Analysis of the population viability in the Carolinian region 14
1.3.4 Critical Habitat 14
2 References 16
Figures 17
Tables 17

Notice

The results provided in this report are subject to an unknown degree of uncertainty. There is substantial uncertainty in the knowledge of demographic data, such as fecundity, survival and dispersal distances. There is also uncertainty in the habitat suitability models, which may be reflected in an incorrect habitat suitability map. This uncertainty and its propagation over time is partly considered in the demographic and environmental stochasticity of the population model. Due to the stochastic nature of the population models, simulation runs were replicated up to 1000 times and results are averages out of those replicate simulation runs. Absolute numbers should be interpreted with caution. Instead trends and differences between different simulation runs (scenarios) are generally more trustworthy. All information used in this work have been discussed with members of the recovery team and verified as well as substituted from the scientific, peer-reviewed literature. The work therefore represents our best possible educated "guess" based on our current knowledge of the biology, life history and habitat requirements for this species.

1 Prothonotary Warbler *(Protonotaria citrea)*

1.1 Demography

The demographic characteristics for the Prothonotary Warbler (PROW) in the Carolinian Region in southern Ontario have been compiled based on published data from the literature and in collaboration with the Recovery Team, in particular Jon McCracken. See also the following references for life-history information on the PROW (Blem et al. 1999, Flaspohler 1996).

Characteristic	Observation	References
Breeding period (ON)	mid-May to mid-July	Petit 1999
Clutch size	5 (typical range 3-8, average 4.5) Clutch sizes are larger in northern than in southern portions of range.	Peck and James 1987 Petit 1999
Broods/year (PA)	1.2	McCracken, unpubl. data
Incubation period	12 days	McCracken, pers. comm.
Fledging period	10-12 days	McCracken, pers. comm.
Maturity	after 1 year	McCracken, pers. comm.
Life Span	8 yrs maximum, 2.5 yr estimated average	Petit 1999
Fledging Success	Tennessee: mean # of young produced per pair per season was 3.9 from mean of 6.5 eggs produced. translates to a 60% rate of fledging success.	Petit 1989
Nesting Success (ON)	44% to 62% (mean 57%) of nests fledge at least one young	McCracken, unpubl. data
Ontario Population Size	24 pairs + 8 unmated males (2002)	McCracken, unpubl. data
Stage/Age class	juvenile / adult	McCracken, pers. comm..
Annual Survival	juvenile 0.24 ± 0.024; adult 0.47 ± 0.047	Petit 1999
Dispersal/Movement	max. 120 km	McCracken, unpubl. data
Average Territory Size	avg. 2-5 ha	McCracken, unpubl. data
Habitat Requirements	highly specialized in low rotting trees with shallow cavities in swampy lowland deciduous forests and woodlands subject to flooding, standing of flowing water and some canopy cover, presence of moss	McCracken, pers. comm.
Threat	habitat loss and disturbance on breeding and wintering grounds, forestry practices, cowbird parasitism	McCracken, pers. comm.
Sex Ratio	30 % more males than females, 43.5 % females	McCracken, pers. comm.
Carrying Capacity in the Carolinian Region (Rondeau)	80 breeding pairs (estimated)	McCracken, pers. comm.
Trend in Population size	decline from 60 to 80 pairs (1980) to about 15 pairs (1996), increase from 15 to 24 pairs from 1996 to 2002	McCracken, pers. comm.

Table 1: Life history data for the Prothonotary Warbler

1.2 Population Model

1.2.1 Model Characteristics

Two software programs RAMAS® GIS (Akçakaya and Root 2002) and PATCH (Schumaker 1998) were used to model the population dynamics of the Prothonotary Warbler. RAMAS® GIS provides a comprehensive set of tools to evaluate the viability of a population or a metapopulation, i.e. a population of populations, of which some may become extinct and re-colonized in isolated habitat fragments. PATCH allows to define and simulate a population model in terms of single individuals, which operate in a spatial, territorial environment. Both software programs allow to analyze the viability of populations and to rank the corresponding relative importance of habitat areas.

1.2.2 Parameter Values

A population model is defined by its conceptual structure (e.g. presence/absence, age classes, individual based) and by its parameter values. Latter must be defined based on the biology and life history of the species of interest.
For the PROW fecundity rates per female have been extracted from the literature and confirmed by the Recovery Team, in particular Jon McCracken. According to data published for the PROW by Petit (1999), the mean number of juveniles produced per pair per season was 3.9 (n=39). This fecundity rate already incorporates nesting success. The observed fecundity rate per successful pair without considering nest success was 5.5 (n=24). According to the literature, the results of this study can be regarded as a conservative estimate for the Carolinian region, because clutch sizes of the PROW are known to be larger in the northern portions than in the southern portions of the PROW range.
The estimated annual survival rates per adult female is 0.47 (n=199). According to McCracken (pers. comm.), the juvenile survival rate is believed to be 50% of the adult survival rate. The parameter values used in the population model are listed in Table 2.
The population model is a “female only” model and the results are based on the number of females. The lower proportion of females in the population (uneven sex ratio, see Table 1) is reflected in the adult fecundity rate. This adjustment (see Table 2) implies that the number of female offspring is less than 50 percent. Another reason for the uneven sex ratio may be a lower survival probability for female adults. If this is the case, the model will slightly underestimate the fecundity of the population resulting in conservative results with respect to the viability of the population.

Parameter	Value/Range	Comments
stage classes	juvenile/adult	McCracken, pers. comm.
juvenile fecundity	0	
adult fecundity	2.036 ± 0.2 (10% stddev.)	1.2 (brood) * 3.9 (fledglings/pair/season) * 0.435 (sex ratio)= 2.036
juvenile survival	0.24 ± 0.048 (2% stddev.)	McCracken, pers. comm.
adult survival	0.47 ± 0.094 (2% stddev.)	McCracken, pers. comm.
density dependence	ceiling exp. growth up to carrying capacity of 80 breeding pairs	McCracken, pers. comm.
simulated years	100	
initial population size	24	McCracken, pers. comm.
replicates (# of simulation runs)	1000	
dispersal	negative exponential up to 100 km	McCracken, pers. comm.
demographic stochasticity	yes	number of survivors and dispersers (emigrants) to be sampled from binomial distributions, number of young from a Poisson distribution. (important for small population sizes)
environmental stochasticity	lognormal	statistical distribution (normal or lognormal) to be used in sampling random numbers for vital rates

Table 2: Parameter values for the PROW population model (RAMAS© GIS)

1.2.3 Analysis of the demographic population viability (non-spatial)

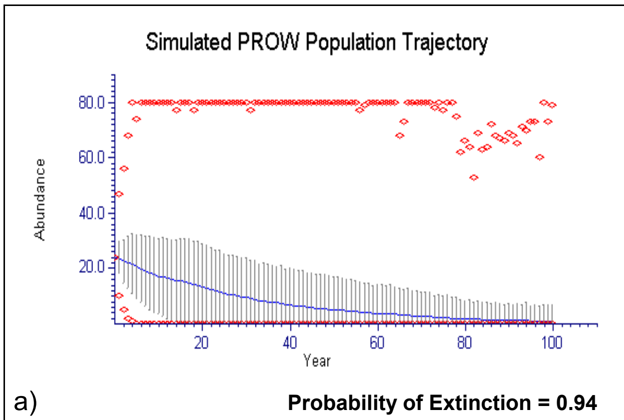
The viability of a non-spatial PROW population was analyzed based on the model parameter values presented in 1.2.2 using RAMAS© GIS. This non-spatial population model assumes that all breeding females reside in one single habitat patch (a cluster of adjacent territories). No dispersal was required and the population could grow exponentially up to a carrying capacity of 80 individuals. The results of this non-spatial population model identify the demographic viability of the population and will serve as a benchmark for the results of subsequent spatially explicit population and habitat viability analyses. The results are presented in Figure 1.

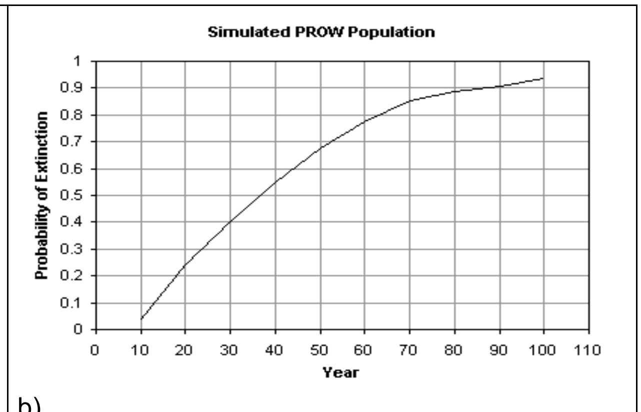
The graph Figure 1a shows the average population abundance over the time span of 100 years. The vertical lines indicate the range of the standard deviation and the red trapeziums show the observed maximum and minimum values. The maximum values are cut off at the carrying capacity of 80 individuals (breeding pairs). The simulation results predict a distinctive population decline on average down to 1 female individual over 100 years. The predicted probability of extinction (or extinction risk) is 94 percent. The extinction risk is calculated as the proportion of replicate simulation runs in which the population became extinct. In this case the population went extinct in 940 out of 1000 replicate simulation runs.

The graph in Figure 1b shows the extinction risk as a function of time. Due to the proliferation of uncertainty and the accumulated effects of stochastic events throughout the course of the simulation (and also in nature), the extinction risk increases over time. The results indicate a low extinction risk for a time span of up to ten years and a 94 percent risk of extinction after 100 years. These numbers are based on the initial population size of 24 breeding pairs and a carrying capacity of 80 breeding pairs.

The graph in Figure 1c shows the minimum viable population size (MVP) for a 99 percent viable population (extinction risk of less than 1 percent) over different time spans. For example, an initial population size of 24 breeding pairs is required to realize a 99 percent viable population over a time span of 6 years. This initial population of 24 breeding pairs would decline during the 6 years to a final population size of 20 pairs.

The results of this non-spatial population viability analysis indicate that the PROW population in Canada, according to our current understanding of the local life history and carrying capacity, is demographically limited and not intrinsically self-sustainable. The PROW population is likely to decline without continual immigration from external populations residing south of the Canadian border.





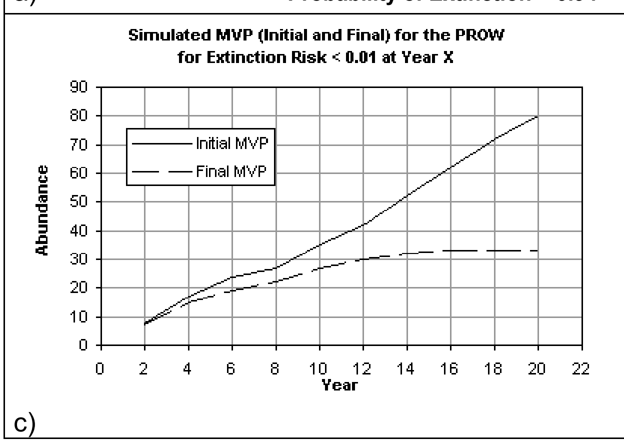


Figure 1:

a) **Predicted population (females only) abundance over 100 years (based on initial population size of 24 females and carrying capacity of 80 females);**

b) **Probability of Extinction over 100 years;**

c) **Minimum viable population (MVP) size. Solid line shows initial MVP and dashed line shows final MVP.**

Predictions from PATCH

Population dynamics for the PROW have also been simulated with the individual based, spatially explicit population model PATCH. The model parameters correspond to those used in RAMAS© GIS (see Table 2). All 80 available territories (carrying capacity) were grouped adjacent to each other into one circular patch of habitat. This setting allows movement between territories only, but does not require movement across non-habitat. It is therefore the closest approximation to a non-spatial setting as used in RAMAS© GIS. The predicted projection of the population abundance over 100 years is shown in Figure 2. The predicted decline in population abundance is similar to those calculated by RAMAS© GIS, but with a more exponential shape of the graph.

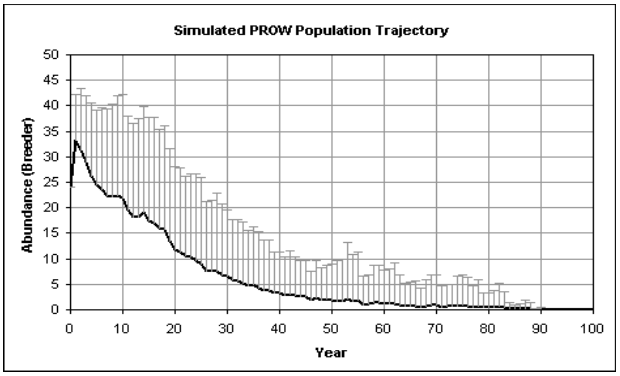


Figure 2: Population abundance for the Prothonotary Warbler in non-fragmented habitat simulated with PATCH. Standard error bars are symmetric and are shown for one direction only. The initial peak in the abundance is attributed to the initial distribution of adult individuals only (non-stable initial age abundance distribution).

1.2.4 Immigration and demographic viability

The assumed dependency of the Canadian PROW population on immigration from external populations has been evaluated in a separate simulation experiment. The effect of immigration on the extinction risk of the Canadian PROW population is shown in Figure 3. The simulation results suggest that one immigrating breeding pair (female) per year should be sufficient to eliminate the extinction risk for the PROW population. Even one immigrating pair every 5 years may reduce the extinction risk to near 10 percent.

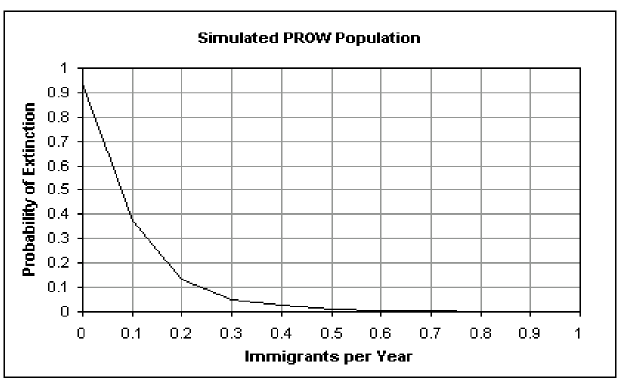


Figure 3: Effect of immigrating breeding pairs from other populations into the Canadian PROW population on the extinction risk. One immigrating breeding pair every two years (0.5 on the x axis) may eliminate the extinction risk.

This quite strong effect of only very few immigrants is surprising. However, these immigrants will reproduce in the population and will boost the overall fecundity of the population, which seems to be lower in the northern range (based on fewer broods per year per female) of the species distribution and responsible for the low viability of the PROW population in Canada.

1.2.5 Habitat Configuration Analysis

The effects of habitat amount and fragmentation have not been considered in the previous non-spatial population viability analysis. The amount of habitat necessary to support a viable population can be estimated from the minimum viable population size times the average territory area. This extrapolation is appropriate when all territories are equally accessible to all members of the population. Habitat, however, is distributed in space and territories are often not adjacent to each other. In most situations, habitat is fragmented and its accessibility depends in part on the movement or dispersal capabilities of a species. Habitat fragmentation and its effect on population viability have become a major area of interest and research in recent conservation ecology. It has been shown in various studies, that the relative importance of habitat fragmentation depends on the actual amount of habitat in a landscape. The following analysis shall help to understand the effects of habitat amount and fragmentation on the viability of the Prothonotary Warbler based on our current understanding of its population biology.

In order to address this question, 60 simple landscapes have been generated using an algorithm published in Fahrig (1997, 1998), Tischendorf and Fahrig (2000) and Tischendorf (2001). Each landscape consists of 100x100 pixels of 200 meter edge length per pixel. The extent of a landscape is therefore 20 km resulting in an area of 400 square km. The pixel size of 4 ha corresponds roughly to the size of one territory of the Prothonotary Warbler (see 1.1, Table 1).

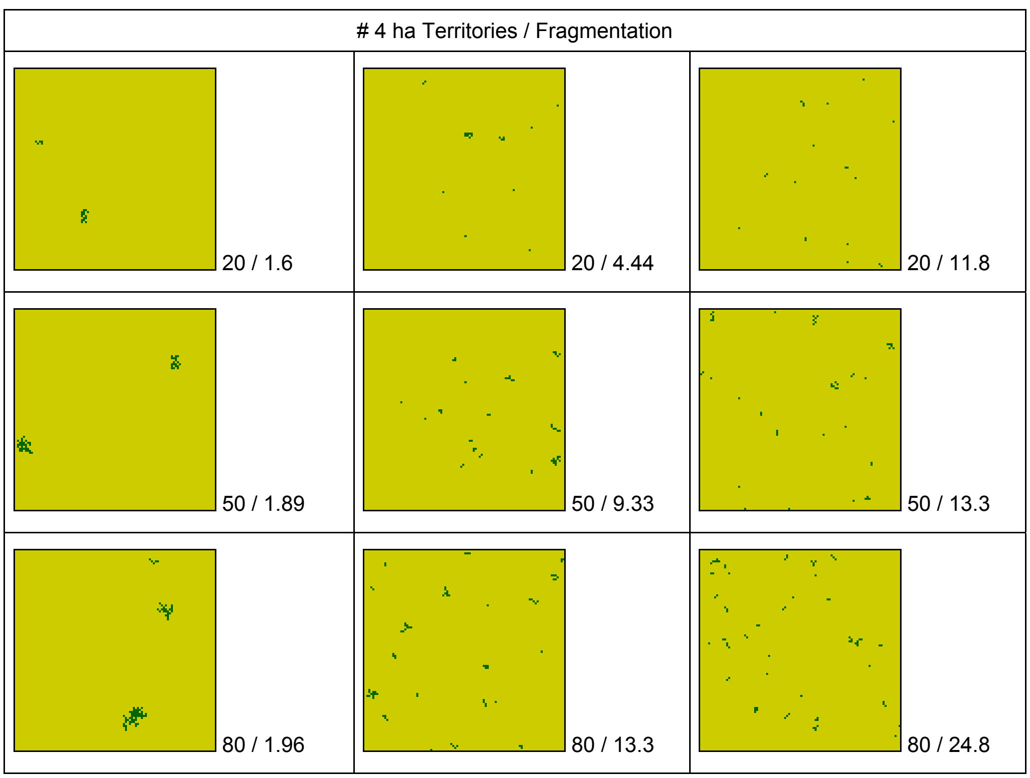


Figure 4: Landscape models used to examine the effect of habitat amount and fragmentation on the probability of extinction for the PROW. Each row shows 3 (out of actually 6) landscapes containing equal, but increasingly fragmented (left to right), amounts of habitat (green/dark areas).

The value of each pixel can either be habitat or non-habitat (matrix). The algorithm used for generating the landscapes allows habitat to be distributed across the landscapes in a more or less fragmented way. Some exemplary landscape models are shown in Figure 4. The amount of habitat (or number of 4 ha territories) was varied between 20 and 80 and the fragmentation for each of the habitat levels was varied across 6 levels from low to high. In Figure 4 each row shows from left to right increasingly fragmented distributions of a number of 4 ha territories (or habitat amount). The numbers to the right of the figures show the actual number of 4 ha territories and the degree of fragmentation. Fragmentation was measured using the "effective number of habitat patches (EN)" (whereas patches are adjacent pixels in the model or neighbouring territories in reality). This new measure of fragmentation was recently developed by Jochen Jaeger (Jaeger et al. 2003). EN has the following features: it is an increasing function of the number of patches; it is an increasing function of the similarity of patch sizes; it is conceptually independent of habitat amount; and it is independent of patch shape and dispersion.

On each of the 60 generated landscapes the population model of the PROW as described in 1.2.1 was executed using RAMAS© GIS. The population was initially distributed across all territories (habitat pixels in the generated landscapes). The carrying capacity was identical to the number of territories and the initial total population size was half the carrying capacity for each landscape. In addition to the non-spatial model described in 1.2.1, individuals were allowed to move within the landscapes. The maximum dispersal distance of the PROW was estimated to be 20 km. (This distance is lower than the maximum distance observed in nature (see Table 1), but corresponds to the 20 km extent of the generated landscapes). This distance was used as a maximum in a negative exponential function. Probability of extinction was measured for each simulation and subsequently related to habitat amount (number of 4 ha territories) and habitat fragmentation (EN, see above). The results are shown in Figure 5-7.

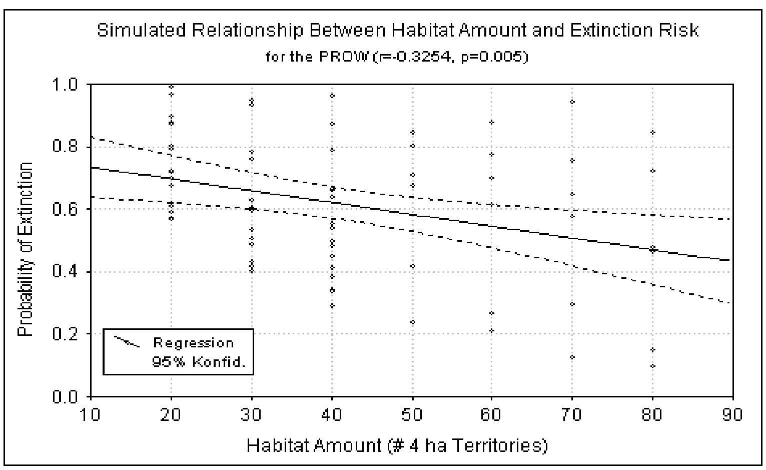


Figure 5: Effect of habitat amount on the probability of extinction. The probability of extinction increases with decreasing habitat amount, but is affected by the spatial distribution of habitat as indicated by the dispersion of the plots.

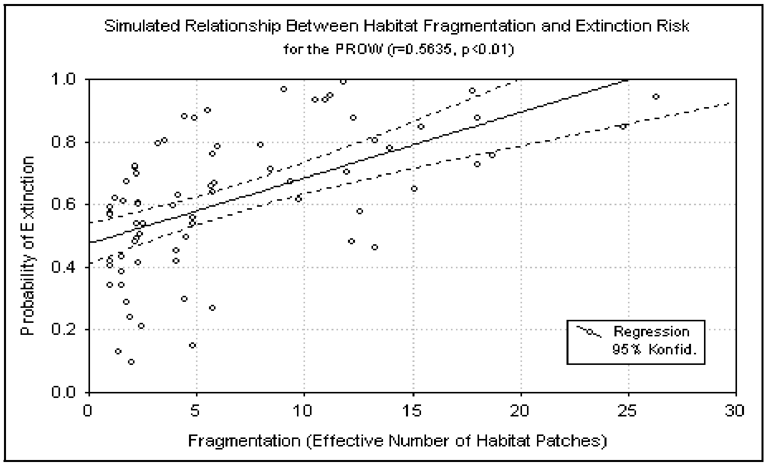


Figure 6: Effect of habitat fragmentation on the probability of extinction. Increasing habitat fragmentation results in overall higher extinction risk, but also depends on the amount of habitat in the landscape.

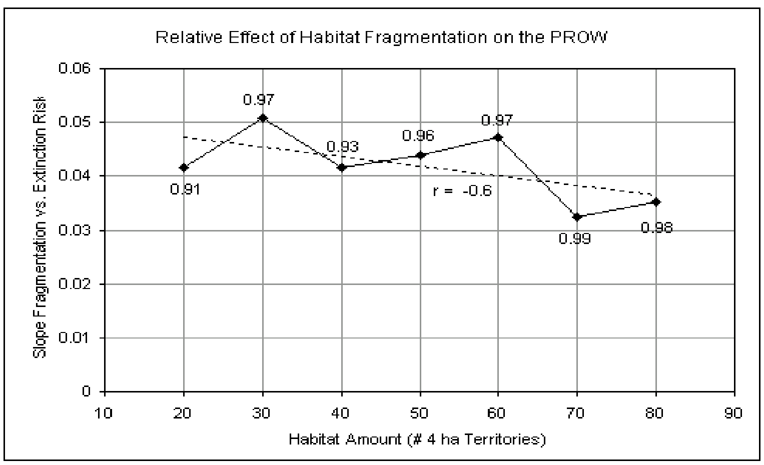


Figure 7: Interaction between habitat fragmentation and habitat amount. The data points are the slopes of the regression lines between habitat fragmentation (EN, see above) and the probability of extinction. The numbers at the plots show the corresponding correlation coefficient r, for the regressions. All regressions were significant at p=0.05. (although some of the relationships are non-linear). The slope of the regression between fragmentation and extinction risk increases slightly with decreasing habitat amount.

The results of this habitat configuration analysis indicate that a) habitat loss increases extinction risk, b) habitat fragmentation increases extinction risk and c) the effect of habitat fragmentation on extinction risk increases with decreasing habitat amount. Matrix quality, roads or landscape topography may still affect and challenge these relationships. The general pattern, however, is in line with the results of many other fragmentation studies.

1.3 Critical Habitat Analysis

1.3.1 Habitat Suitability Map

The critical habitat analysis for the PROW in the Carolinian region is based on the habitat suitability map as shown in Figure 9. This map has been produced based on the currently known habitat preferences of the PROW. (documentation of the habitat suitability model will be provided by Mike Flaxman) The geographical context for the habitat suitability map is shown in Figure 8. The occurrence range of the PROW in southern Ontario is restricted to this area, which is bordered by Lake Ontario, Lake Erie and Lake Huron. Major urban areas are Toronto and Hamilton (east), London (central) and Windsor (west).

The habitat suitability map for the PROW (Figure 9) contains 3 land cover types: no habitat, occupied habitat and unoccupied habitat. The occupied habitat comprises those areas, which were identified as habitat and which have been occupied by the PROW. The unoccupied habitat shows those areas, which meet the known habitat requirements for the PROW, but which have not been occupied by this species.

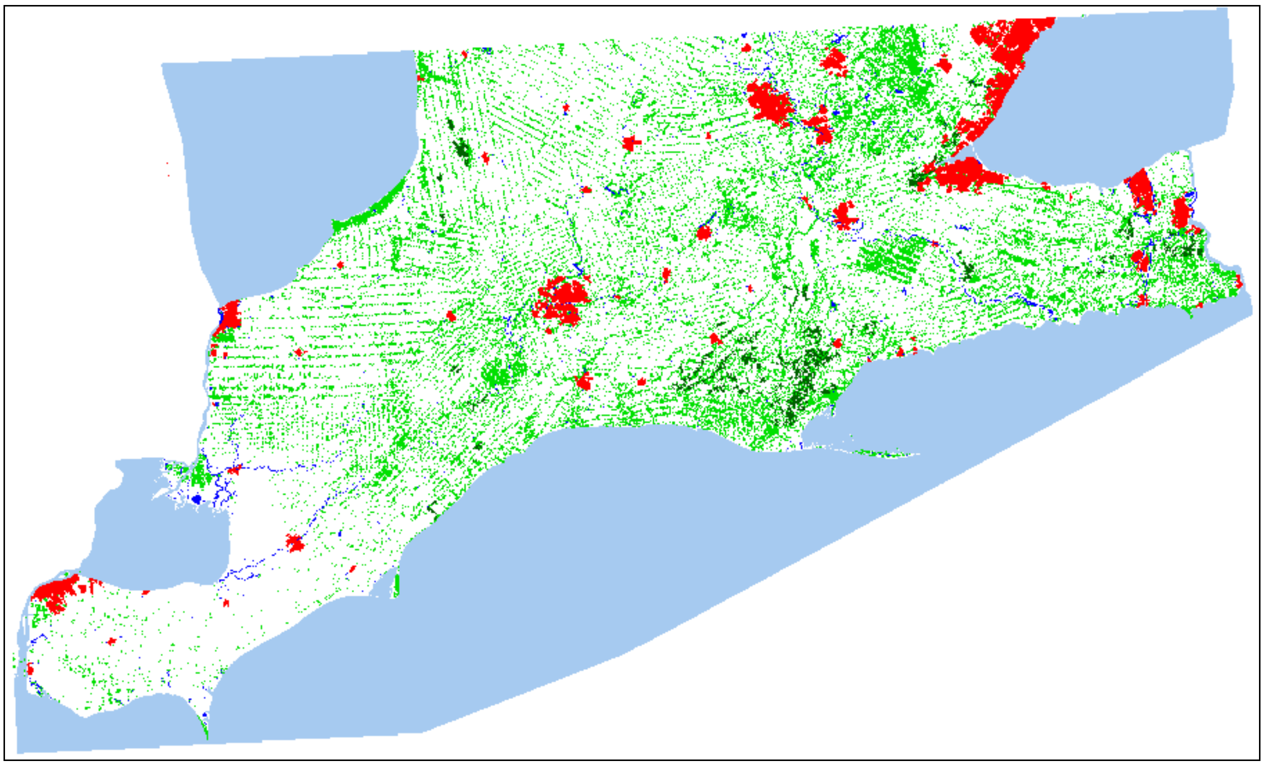


Figure 8: Study area and occurrence range of the PROW in southern Ontario.

The habitat suitability map as shown in Figure 9 has the following characteristics:
north-south extent = 203 km, east-west extent = 400 km, pixel size = 95.26m x 95.26m (9074.250 m²),
map size = 4193 x 2134 pixels, total area = 81200 km², occupied habitat area = 140 km²,
unoccupied habitat area = 576 km².

The habitat suitability map as shown in Figure 9 was aggregated into a coarser resolution, because the number of occupied and unoccupied habitat patches (pixel clusters) was too large to be processed with RAMAS© GIS. The resolution was therefore changed by factor 12 using a pixel thinning algorithm. This algorithm was chosen because it preserved the proportions of each land-cover type in the aggregated maps. The aggregated habitat suitability map used for the population models has the following characteristics: pixel size = 1143m x 1143m (1.306 km²), map size = 349 x 177 pixels.

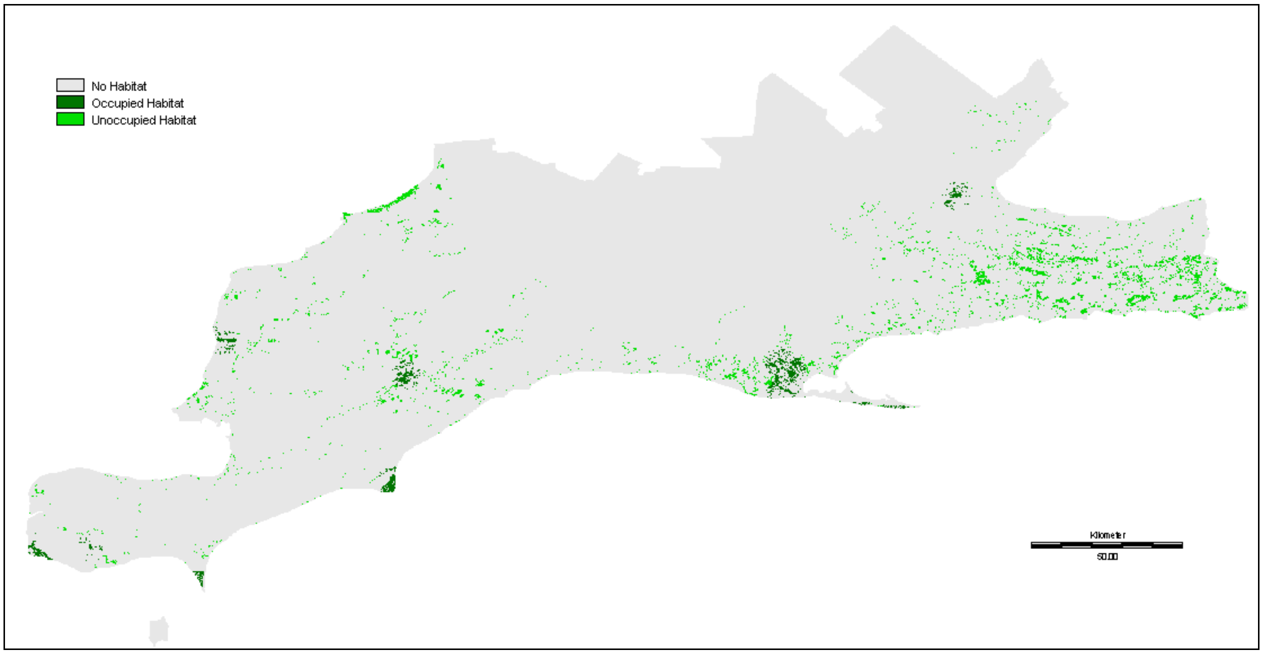


Figure 9: Habitat suitability map for the Prothonotary Warbler (400 x 203 km)

1.3.2 Source – Sink habitat

The spatially explicit and individual based population model PATCH was used to rank habitat according to recorded average occupancy and net emigration rates. Higher occupancy rates indicate more sustainable populations. Higher net emigration rates indicate source habitat.

The population model as described in 1.2 (Table 2) was applied to the habitat suitability map as shown in Figure 9. In a first step, occupied habitat was extracted from the habitat suitability map and simulations were conducted on occupied habitat only. In a second step, simulations were conducted on all occupied and unoccupied habitat. Initial populations were seeded in locations, which were occupied in 2002. Reproduction was restricted to habitat area, whereas movement (dispersal) could occur in non-habitat. Individuals could move up to 100 territories, which corresponds to the observed movement/dispersal distance of about 120 km. Moving individuals chose the closest available territory while moving. (Note, patch allows to set the movement mode to 'random walk', 'optimal' and 'closest') Since no data are available for the territory selection of the PROW and random walk is unlikely, individuals are assumed to chose the closest available territory while moving. A sensitivity analysis between the 'optimal' and 'closest' movement mode showed slight but insignificant differences in the model output.

Side fidelity for adult individuals was set to medium out of the options 'low', 'medium' and 'high'. Simulations were conducted for 100 time steps (years) and replicated 100 times. Patch records occupancy rates, emigration and immigration rates into patches among other demographic measures. The results are illustrated in Figure 10 and 11.

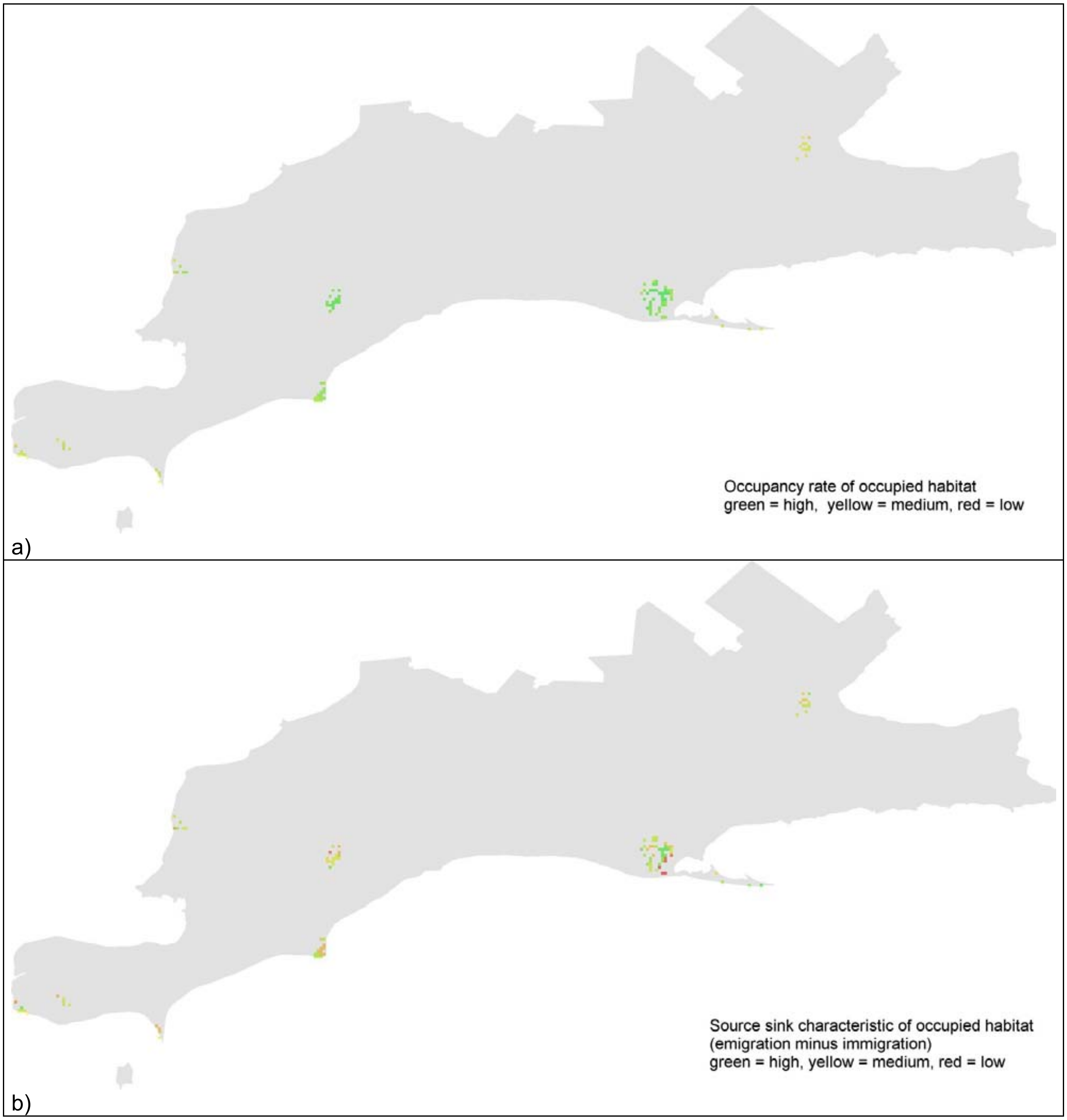


Figure 10: Occupancy rates and source – sink characteristics for occupied habitat.

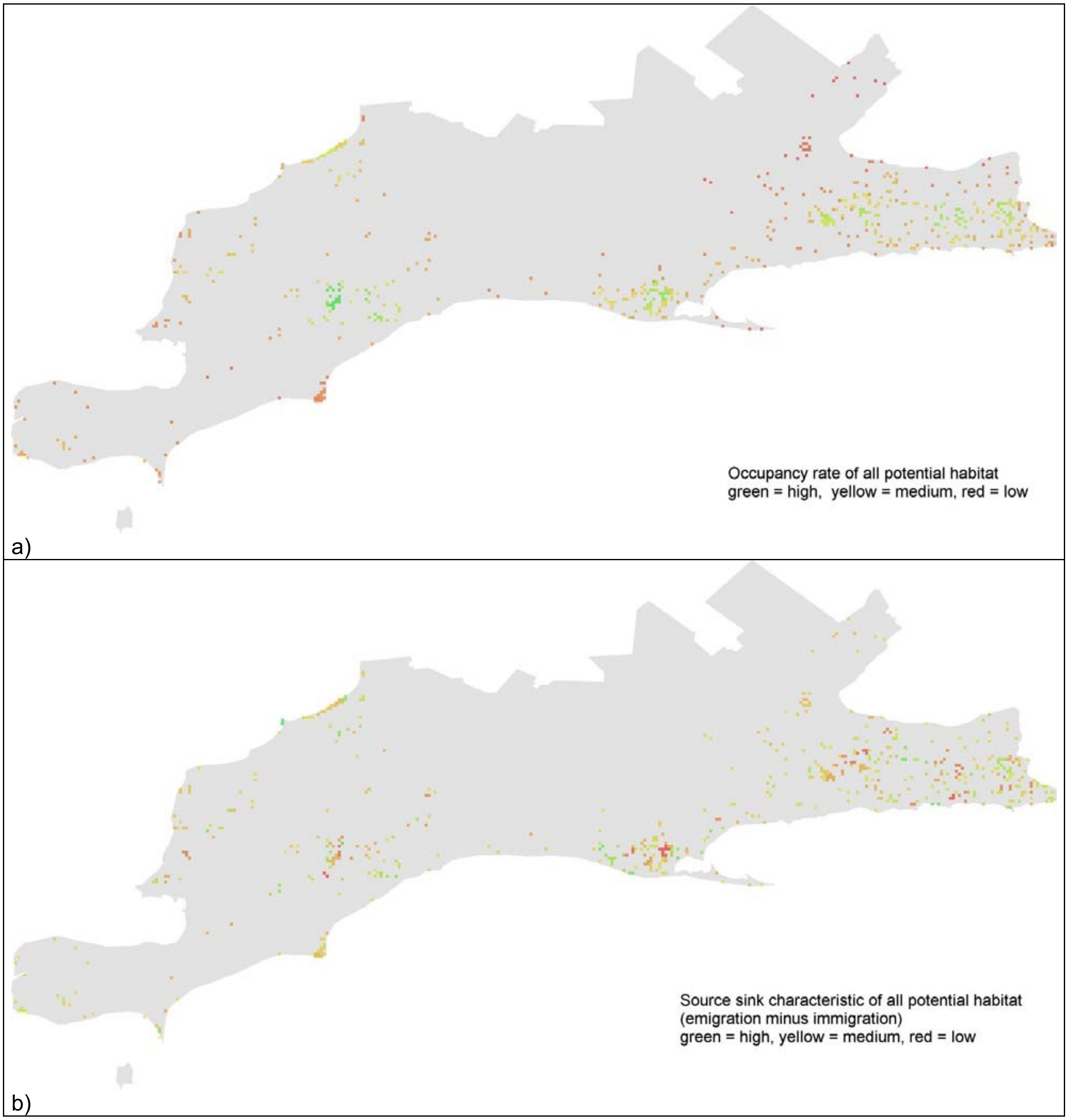


Figure 11: Occupancy rates and source – sink characteristics for all identified suitable habitat

The green areas indicate higher occupancy and net emigration rates, whereas yellow or red areas indicate lower rates. The maps in Figures 10 and 11 show that larger patches, which are also close to each other have the highest occupancy rates and serve as sources for smaller or peripheral territories. Those areas should therefore be regarded as most critical for the viability of the PROW population.

1.3.3 Analysis of the population viability in the Carolinian region

The population model as described in section 1.2 was applied to the habitat suitability map using RAMAS© GIS in order to estimate the viability of the PROW population based on the habitat configuration in the Carolinian region. The simulation procedure corresponds to those used in the habitat configuration analysis (see section 1.2.5). Simulations were conducted on occupied habitat only and on all identified suitable habitat as shown in Figure 9. The results are shown in Figure 12.

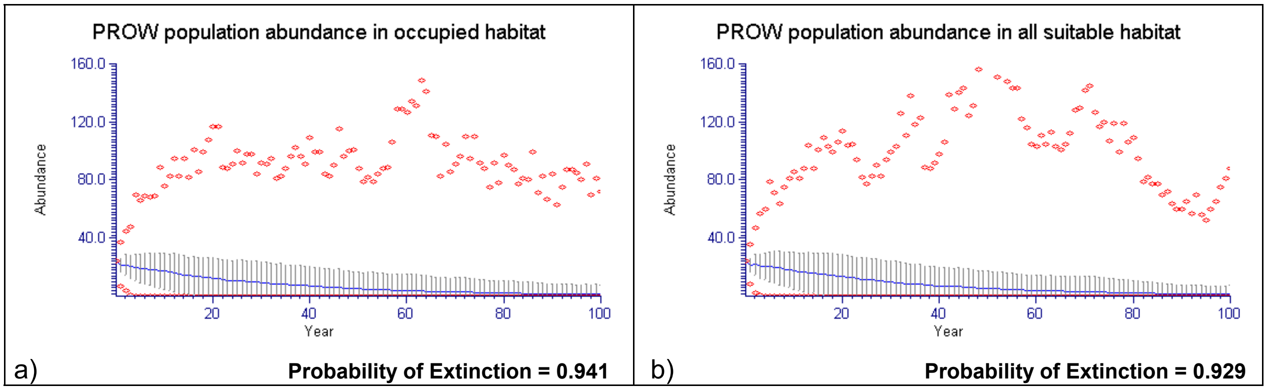


Figure 12: Extinction risk and predicted population abundance for the PROW in the Carolinian region when residing in occupied habitat only (a) and when using both occupied and potential suitable habitat (b).

The results of the simulated population dynamics on the habitat suitability map indicate a population decline and a high extinction risk for the PROW population over a time span of 100 years. The maximum recorded population abundances are near 100 individuals and slightly higher when all suitable habitat can be used (compare Figure 12 a and b). Extinction risk is slightly lower when all suitable habitat is available. Overall, the results are almost identical to those obtained from the initial, non-spatial analysis of the demographic viability of the PROW population (see section 1.2.3). This indicates and confirms that the demographic limitation may by far offset limitations caused by habitat configuration, such as habitat amount and fragmentation. It is still possible, however, that habitat quality in the Carolinian region (in addition to possible climatic constraints) is the main reason for the lower demographic potential of the PROW population.

1.3.4 Critical Habitat

In order to identify the most critical habitat patches (in addition to the source-sink ranking as shown in Figures 10 and 11), a patch-removal experiment was conducted. The population dynamics of the PROW were simulated on the habitat suitability map using RAMAS© GIS. Several replicate simulation runs were conducted while each time one patch was removed. The difference in the risk of extinction resulting from simulations on all habitat patches and those from simulations where one patch was removed indicate the relative importance of the habitat patch for the extinction probability. Patch size was also considered in ranking the criticality of the habitat patches. In the resulting critical habitat map (see Figure 13) all those patches are categorized as critical (and marked in red colour), which are either larger than 5 km² or which reduce the extinction risk by more than 2 percent. Note that this categorization is arbitrary and for the purpose of highlighting the most critical habitat patches. Criticality is actually directly proportional to the relative importance of a patch to the extinction risk and to its size.
This experiment was conducted on the occupied habitat map only. The results are shown in Figure 13.

The results indicate that the largest patches have the strongest effect on the extinction risk and must therefore be regarded as critical habitat. The most important habitat patch (25 in Figure 13a) is Rondeau Provincial Park at Lake Erie. This area accounts for 20 percent of the viability of the PROW population. In other words, removing this habitat would increase the extinction risk of the PROW population by 20 percent. The second most important habitat patch is Amherstburg in Essex county (30 in Figure 13a). This area accounts for about 8 percent of the PROW population viability. Other areas are larger but less critical. Note that this ranking is based and highly dependent on the initial seeding locations for the populations in the model. Occupancy locations from 2002 were used to distribute the initial 24 females across the habitat area in the habitat suitability model. Habitat patches with initial population sizes greater than zero will have a stronger effects on the extinction probability compared to those, which are not occupied initially. This applies in particular for the PROW population, which may not have the capability to colonize all available habitat over time due to its demographic limitation.

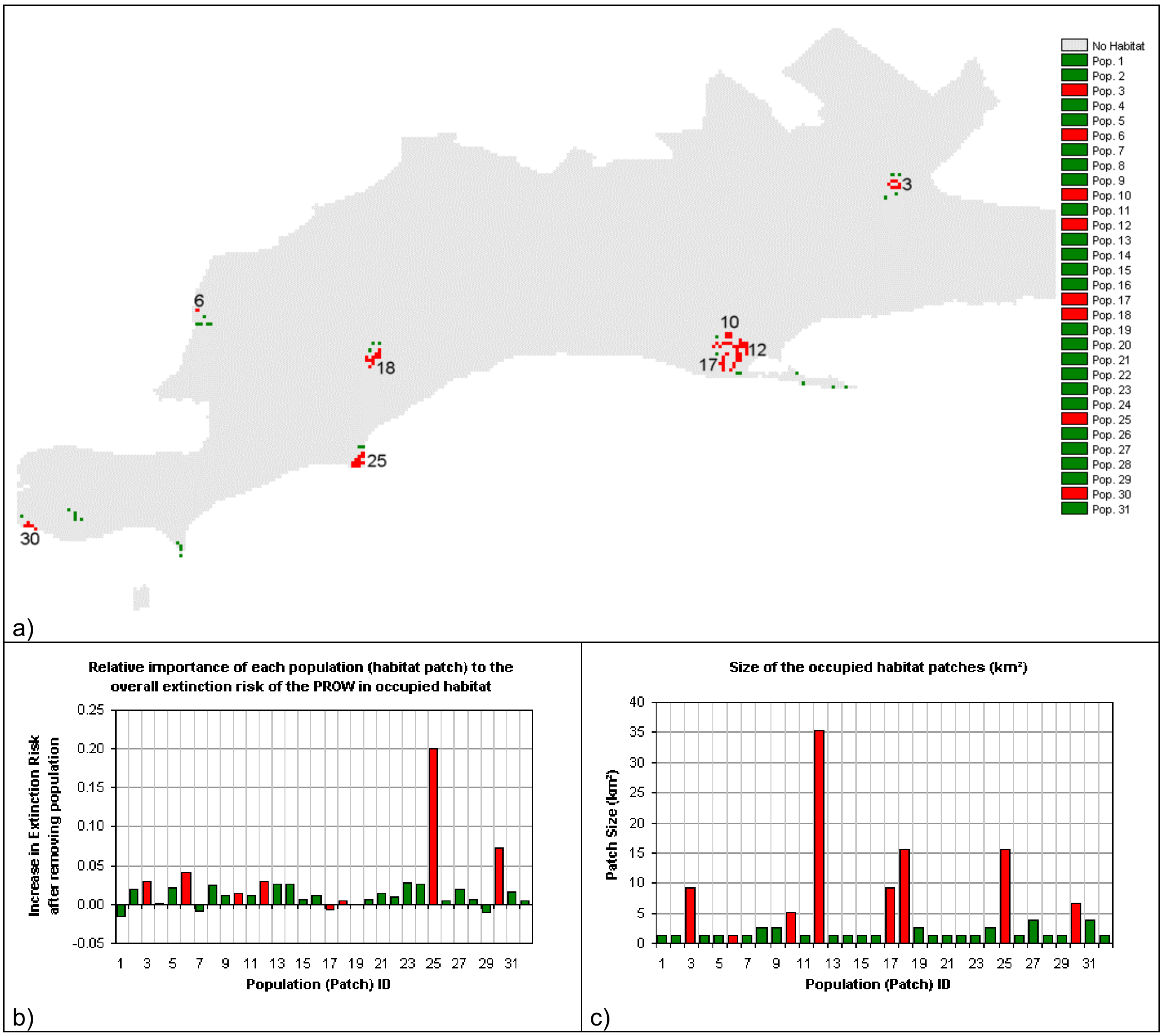


Figure 13: Relative importance of <u>occupied</u> habitat patches to the extinction risk of the PROW populations. a) Most critical habitat patches are marked in red colours in the critical habitat map. b) Relative importance of the habitat patches to the extinction risk. c) Sizes of the habitat patches.

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Figures

Figure 1:.. 5
Figure 2: Population abundance for the Prothonotary Warbler in non-fragmented habitat simulated with PATCH. Standard error bars are symmetric and are shown for one direction only. The initial peak in the abundance is attributed to the initial distribution of adult individuals only (non-stable initial age abundance distribution)... 6
Figure 3: Effect of immigrating breeding pairs from other populations into the Canadian PROW population on the extinction risk. One immigrating breeding pair every two years (0.5 on the x axis) may eliminate the extinction risk... 6
Figure 4: Landscape models used to examine the effect of habitat amount and fragmentation on the probability of extinction for the PROW. Each row shows 3 (out of actually 6) landscapes containing equal, but increasingly fragmented (left to right), amounts of habitat (green/dark areas). 7
Figure 5: Effect of habitat amount on the probability of extinction. The probability of extinction increases with decreasing habitat amount, but is affected by the spatial distribution of habitat as indicated by the dispersion of the plots. 8
Figure 6: Effect of habitat fragmentation on the probability of extinction. Increasing habitat fragmentation results in overall higher extinction risk, but also depends on the amount of habitat in the landscape. . 9
Figure 7: Interaction between habitat fragmentation and habitat amount. The data points are the slopes of the regression lines between habitat fragmentation (EN, see above) and the probability of extinction. The numbers at the plots show the corresponding correlation coefficient r, for the regressions. All regressions were significant at p=0.05. (although some of the relationships are non-linear). The slope of the regression between fragmentation and extinction risk increases slightly with decreasing habitat amount. 9
Figure 8: Study area and occurrence range of the PROW in southern Ontario... 10
Figure 9: Habitat suitability map for the Prothonotary Warbler (400 x 203 km) 11
Figure 10: Occupancy rates and source – sink characteristics for occupied habitat. 12
Figure 11: Occupancy rates and source – sink characteristics for all identified suitable habitat................ 13
Figure 12: Extinction risk and predicted population abundance for the PROW in the Carolinian region when residing in occupied habitat only (a) and when using both occupied and potential suitable habitat (b). 14
Figure 13: Relative importance of occupied habitat patches to the extinction risk of the PROW populations. a) Most critical habitat patches are marked in red colours in the critical habitat map. b) Relative importance of the habitat patches to the extinction risk. c) Sizes of the habitat patches. 15

Tables

Table 1: Life history data for the Prothonotary Warbler 3
Table 2: Parameter values for the PROW population model (RAMAS© GIS)... 4